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ANATOMICAL AND HISTOLOGICAL STUDIES OF THE FEMALE REPRODUCTIVE ORGANS OF THE AMERICAN SAW-FLY, CIMBEX AMERICANA, LEACH.

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(with plates iii to v.)

The material for the present paper was obtained in Milwaukee County, Wisconsin. The insects were collected during June and the early part of July usually from the peach-leaved willow (Salix amygdaloides Anders.) and the long-leaved willow (Salix longifolia Muhl.)

ANATOMICAL STRUCTURE OF THE FEMALE REPRODUCTIVE ORGANS.

The internal female reproductive organs of Cimbex occupy the greater part of the abdominal cavity. The paired ovaries, which embrace the dorso-lateral sides of the alimentary canal, are pale greenish in color and extend from the second to the posterior end of the seventh abdominal segment (Fig. 1, *ov*). Each ovary is made up of a large number of ovarian tubules arranged in a parallel manner. Anteriorly, these tubules taper gradually into the very fine thread-like terminal filaments, which are twisted together distally, thus holding the two ovaries together; posteriorly, the tubules of each ovary open into the funnel-shaped oviducts. The two oviducts unite in a forked manner below the alimentary canal to form the common oviduct or oviductus communis. In a dorsal view, the oviductus communis is almost entirely hidden by the spermatheca (Fig. 1, *sp*) and the large reservoir of the colleterial glands (Fig. 1, *cs*). The common oviduct terminates in the vaginal orifice, which is directly below the peculiar notch of the last sternite and the base of the ovipositor (Fig. 16, *vo*).

The spermatheca in the living condition is of a pale yellowish color, but in the material injected with 95 per cent. alcohol, it assumes a whitish color. From an external view, a constriction divides the seminal receptacle into two parts: (1) a more or less heart-shaped dorsal part (Fig. 1, *sp*); and (2) a funnel-shaped ventral portion, which opens into the dorsal wall of the common oviduct (Fig. 18, *f*). This boundary is further marked by two bundles of transverse muscles, which leave the spermatheca on either side and attach to the body wall. The musculature of the spermatheca and the function of these will appear in a subsequent paper.

In order to ascertain the exact course which the male intromittent organ takes during copulation, the abdomen of a number of specimens was cut in two during the sexual union and then dropped into 95 per cent. alcohol. If, after thorough dehydration, the abdomen of the male and female are separated, the opening in the female for the reception of the male organ can be distinctly seen to be directly beneath the peculiar notch of the last sternite (Fig. 16, *vo*). A careful dissection of the abdomen of two specimens obtained in this manner shows that the male copulatory organ passes not only into the common oviduct, but extends for some distance up into the funnel-shaped portion of the spermatheca.

The accessory glands consist of a mass of coiled tubes lying for the greater part dorsal and lateral to the colleterial sac and spermatheca. A dissection of an insect immediately after it has been killed, shows that the accessory sac and glands are filled with a rather thick translucent liquid. With the addition of alcohol this liquid hardens, forming a whitish solid. In Fig. 1, the accessory glands were teased away from the reservoir and receptaculum seminis. These glands, when they are spread apart, are found to be composed of a right and left mass of branching tubules, which terminate blindly in slightly swollen ends. The branching tubules composing these masses finally communicate with two long unbranched ducts, the right and left accessory gland ducts. These ducts, in turn, unite a short distance before joining the colleterial sac, forming a broad duct, the common colleterial gland duct, which communicates with the reservoir posteriorly (Figs. 17 and 18, *ccd*). The colleterial reservoir is a large slightly bilobed sac (Fig. 1, *cs*) which opens to the outside at the base of the saws by a broad, somewhat obliquely inclined duct (Figs.

13 and 18, *d*). Near the opening of the duct are two bundles of transverse muscles, which leave the dorsal wall of the duct and attach to the basal margin of the sheaths of the saws (Figs. 13 and 17, *tm*). Dorsally, the colleterial duct is in continuation with two lobes (Fig. 13, *dl*) which, in turn, are in continuation with the membrane that lines the inner surface of the saws. Ventrally, the wall of the duct terminates in a large fold (Figs. 13 and 18, *vf*). The duct of the colleterial sac thus opens out between the two dorsal lobes and the large ventral fold (Fig. 13, *d*).

When the spermatheca and colleterial sac are carefully pulled away from each other, there is revealed a triangular chitinous plate, which rests upon the dorsal wall of the oviductus communis. To this plate several bands of muscle attach (Fig. 13, *tp*).

HISTOLOGICAL STRUCTURE OF THE FEMALE REPRODUCTIVE ORGANS.

Ovaries: Each ovary is made up of a variable number of ovarian tubules or ovarioles, there being usually between twenty and thirty. In six specimens dissected, the number of ovarian tubes in the entire ovary was neither constant nor equal in either ovary, as is shown by the following figures:

Ovarioles in Right Ovary.	Left Ovary	Total in Both.
28	23	51
21	23	44
27	25	52
25	27	52
25	24	49
30	28	58
Average, 26	25	51

When the lowest egg in each tubule is ripe or nearly so, it is elongated more or less ovoid in shape with the distinction between dorsal and ventral surfaces indicated by a difference in curvature. After the lowest egg in each ovariole has passed out of the egg-tube, each tubule appears to be supported upon a stalk which opens into the oviduct. Alternating with each egg-chamber is a nutritive or yolk-compartment, the latter being distinguishable from the former with the naked eye only at the basal end of the ovarian tubule by its smaller size. The nutritive chamber, which is anterior to the basal egg, is usually smaller (Fig. 1, *nc*) than the one between the next two eggs. Towards the distal end of the ovariole, however, egg-chambers and yolk-chambers cannot be distinguished as such with the naked eye by a difference

in size. The tip of the egg-tube passes over gradually into the terminal chamber, which, in turn, passes over into the terminal filament.

A histological study of the wall of the egg-tube shows that it is covered externally by a peritoneal membrane, in which anastomosing, transversely-striated muscle fibres are embedded. Toward the distal end of the ovariole, the peritoneum is especially well developed, while posteriorly it gradually becomes thinner. The anastomosing muscles extend to the apex of the ovariole, being present in even the terminal filament. Within the peritoneum is a basement-like membrane; this membrane is sometimes distinctly visible between the nutritive and egg-chambers.

Oviduct and Oviductus Communis: In general, the histological structure of the oviduct will hold good also for the oviductus communis anterior to the spermatheca. The following layers, passing from within outward, are present: (1) a chitinous intima; (2) an epithelial layer; (3) a longitudinal muscle layer; (4) a circular muscle layer; and (5) a peritoneal membrane (Fig. 5).

When no eggs are present in the oviduct or oviductus communis, their wall is thrown into folds which are nearly filled with longitudinal muscles (Fig. 5, *lm*). The chitinous intima varies but little in thickness throughout the entire genital duct; such variations as occur are found directly beneath the egg-tubes, where the chitin is extremely thin and hardly perceptible. A surface view of this intima shows the presence of long, yellowish, chitinous bristles which are not distributed uniformly, but are clustered in groups (Figs. 3 and 5, *b*). The epithelial cells, with cell boundaries usually indiscernable, contain a large ovoid nucleus embedded in a slightly granular cytoplasm. External to the epithelial layer are the longitudinal muscles, which are somewhat better developed than the circular muscles just outside of these.

Spermatheca: A longitudnial section through the spermatheca shows that the structure of the chitinous intima is somewhat similar to the chitinous integument which Folsom (16) described for most insects. He writes: "The chitinous integument (Fig. 88) of most insects consists of two layers: (1) an outer layer, homogeneous, dense, without lamellae or pore canals, and being the seat of the cuticular colors; (2) an inner layer, 'thickly pierced with pore canals, and always in layers of different refractive indices and different stainability.' (Tower.) These two

layers, respectively *primary* and *secondary* cuticula, are radically different in chemical and physical properties." In the heart-shaped dorsal part of the spermatheca numerous pore canals, which stain deeply with gentian violet, penetrate the hyaline lamellated secondary layer of chitin in a more or less wavy manner (Figs. 4 and 7, *c*). They could, in some cases, be seen to enter the deeply staining primary layer, but could not be traced for any great distance here. In the funnel-shaped ventral portion of the spermatheca the pore canals could not be found.

A number of microscopic differences occur in the two divisions of the spermatheca. In the dorsal region of the heart-shaped part, the primary layer of chitin is smooth and entirely free from bristles (Fig. 7, *p*). At some distance dorsal to the constriction, which marks the boundary between the two divisions of the spermatheca, there are a few sharply pointed bristles scattered about irregularly (Fig. 4, *b*). Near this boundary the primary layer of chitin assumes a folded appearance with the bristles regularly arranged on one side of the fold and pointing ventrally (Fig. 4, *v*). At the constriction, however, the bristles change in direction and point dorsally and they are here arranged on the opposite side of the fold (Fig. 4, *a*). The bristles retain this position throughout the funnel-shaped ventral portion of the spermatheca.

In the dorsal heart-shaped region of the spermatheca the epithelium consists of prismatic cells, where cell boundaries are discernable, while in the funnel-shaped portion the inner ends of the cells vary somewhat in shape, owing to the folding of the chitinous intima. The cytoplasm in the dorsal and throughout the greater part of the ventral divisions of the spermatheca is granular towards the chitinous intima, but towards the basal end, the epithelial cells show a distinct longitudinal striation. Each cell contains an ovoid nucleus with its long axis at right angles to the chitinous intima (Fig. 7).

Near the region where the spermatheca opens into the common oviduct, the epithelial cells gradually become smaller and more or less flattened. The long axis of the ovoid nuclei usually assumes a direction parallel to the chitinous intima. The marked longitudinal striation has disappeared, and the cytoplasm is granular throughout these cells. Both primary and secondary layers of chitin are very much thinner, but the bristles are of the same size and still point dorsally (Fig. 2).

The transition from the spermatheca to the common oviduct is not difficult to determine, the chitin of the former losing its regularly folded appearance, and becoming more or less irregularly folded in the latter. The bristles, which in the spermatheca were regularly arranged on one side of the folds, do not have this uniform arrangement in the oviductus communis, but are clustered in groups (Fig. 3, *b*).

Accessory glands and sac: A study of sections cut through the accessory glands and ducts shows them to consist of the following layers, passing from within, outward: (1) a chitinous intima; (2) the so-called "endothelial or centro-tubular cells" of Fernard (15); (3) an epithelial layer; (4) a basement membrane; and (5) a peritoneal membrane.

Each cell of the accessory glands contains a so-called "vésicule sécrétante or vésicule intracellulaire" of Dierkx (13) or "vésicule radiée" of Henneguy (18). This vesicle is more or less oviform in shape and oftentimes strands of cytoplasm radiate from it (Fig. 9, *vr*). A small chitinous canal [canalicule intravésiculaire of Dierkx (13)] leaves the vesicle, follows a sinuous path to the chitinous intima, which it penetrates, and opens out into the lumen of the gland (Fig. 9, *c*). This canal, or its contents, stains with gentian violet and to a slight extent with haematoxylin. The nucleus is found in the basal half of the cell usually close to the vesicle.

The "endothelial or centro-tubular cells" are represented in Cimbex by nuclei, which are usually crowded against the chitinous intima (Fig. 9, *en*) or wedged in between the inner ends of two glandular cells.

A comparison of a transverse section through the accessory glands with a similar section cut through the right or left colleterial gland duct or the common colleterial gland duct shows some marked differences. The sections show a different stainability, especially with the triple stain. The cytoplasm of the accessory gland cells stains deeply and the vesicle with its canal cannot usually be distinctly seen; in the ducts, however, the vesicle with its canal is well defined, the cytoplasm stains less deeply and shows a distinct longitudinal striation towards the basal end of the cells, but near the chitinous intima this striation is gradually lost and the cytoplasm becomes more homogenous (Fig. 10). In the accessory glands the large nucleus is spherical in shape and is found in the basal region of the cell, while in the ducts the more

or less ovoid nucleus varies in shape and may often be found between the vesicle and the outer boundary of the cell (Fig. 10) or nearer the central part of the cell. In the accessory glands the cell boundaries are very distinct (Fig. 9) but in the ducts these are indiscernable (Fig. 10). The cells of the glands are somewhat larger than those of the duct; the former surround a rather small central lumen, while the lumen of the duct is much larger.

The nuclei of the "endothelial or centrotubular cells," which are usually crowded up against the chitinous intima or wedged in between the inner ends of the two glandular cells in the accessory glands, are found midway in the epithelial layer in the ducts (Fig. 10, *en*). They can be distinguished easily from the nuclei of the epithelial cells by their smaller size.

All of these facts would tend to show that the cells of the right and left colleterial gland ducts, as well as the common colleterial gland duct, have either been emptied of their secretion, or that they have lost their power of secreting. As, however, quite a number of sections were cut through these ducts, and all showed the same structure we are inclined to believe that the cells have given up the secreting function and that the "endothelial or centro-tubular" nuclei have migrated from the position close up against the chitin to one between the cells. To definitely decide this point one would have to work probably with the pupae or larvae.

The histological change from the common colleterial gland duct to the accessory reservoir is rather abrupt. An outer, irregularly branching muscle layer makes its appearance upon the reservoir. The vesicles with their canals and the "endothelial or centro-tubular" nuclei gradually disappear in the sac (Figs. 8 and 11). A noticeable change in the epithelium is also apparent. In the common colleterial gland duct, the cytoplasm shows a distinct longitudinal striation toward the basal end of the cells, but near the chitinous intima the cytoplasm becomes granular; in the accessory sac, however, the cytoplasm is distinctly granular throughout the cell (Fig. 11). The epithelial cells of the colleterial reservoir vary in size, owing to the numerous, small, irregular folds into which the wall is thrown. Sharply pointed spines are present in the sac; these are especially numerous near the entrance of the common colleterial gland duct into the sac, and at the region where the latter passes over into its duct (Fig. 12, *sp*).

A series of transverse sections of the duct of the colleterial sac, shows the presence of a large ventral fold, which is partly filled with muscles and grooved at its middle (Figs. 14 and 15). The epithelial layer is somewhat better developed around this fold than at any other part of the duct. Around this fold the long axis of the ovoid nucleus is at right angles to the chitinous intima, but to either side of the fold, they gradually change their position and assume a direction more or less parallel to the intima (Figs. 14 and 15, *n*). The chitin lining the lumen is extremely thick. Near the opening of the duct are two bundles of transverse muscles which leave the chitinous intima and attach to the basal margin of the sheaths of the saws (Fig. 14, *tm*). These muscles when they contract, aided probably with the elasticity of the thick chitinous intima, close the duct.

A longitudinal section of this same duct shows that the muscles which, as already described from a cross section, partly fill up the large fold, can be traced over from the colleterial sac. Within the fold they spread out fan-like and attach to the chitinous intima (Fig. 12). These muscles when they contract open the duct.

A closer examination of the longitudinal section shows that the wall of the large ventral fold (Fig. 18, *vf*) when traced to the region where the duct opens out, bends upon itself and is continuous with the dorsal wall of the common oviduct. The chitinous intima of the large ventral fold decreases gradually in thickness toward the opening of the duct, and bending upon itself, continues as a layer of chitin of almost uniform thickness to the triangular chitinous plate. (Fig. 18, *chp*) which, as already described, rests upon the dorsal wall of the common oviduct between the spermatheca and colleterial sac. Projecting here and there from this chitinous intima near the opening of the duct of the sac, are long, yellowish bristles. Besides these bristles, large multinucleated glands with a pore canal penetrating the chitinous intima in their neighborhood and peculiar sense organs are scattered between the epithelial cells.

These sense organs project as papillae from the chitinous intima, and are very evident when the colleterial sac duct is mounted *in toto*. At the distal end of these papillae is a ring of chitin enclosing a circular opening. This ring of chitin stains with gentian violet. The papilla is in connection with a clear bladder-like structure, which is surrounded by a somewhat granular pro-

toplasm containing one or more nuclei. Within the clear bladder-like structure is a cone [Achsencylinders of Will (32)] which gradually becomes thicker toward its basal portion. From the basal region of the sense organ a nerve is given off.

The epithelium, when traced from the region where the duct of the colleterial sac opens out, to the triangular plate, is seen to be represented by cells which are somewhat wider than long, with their basal ends more or less rounded. Anterior to the triangular plate, however, there is an abrupt cellular change; the epithelial cells, as already mentioned in the description of the cellular change between the spermatheca and common oviduct, are extremely flattened and are represented chiefly by ovoid nuclei, which are arranged parallel to the chitinous intima (Fig. 3).

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EXPLANATION OF PLATE III.

All figures except general dissections were drawn with a camera lucida.

Fig. 1. Dissection showing dorsal view of reproductive organs with left ovary removed: *ov*, ovary; *nc*, nutritive chamber; *od*, oviduct; *cod*, oviductus communis; *sp*, heart-shaped part of spermatheca; *acg*, accessory glands teased apart; *cs*, colleterial sac; *m*, muscle bundles of saw; *s*, sheaths of saw. (x4.)

Fig. 2. Longitudinal section of cells through the funnel-shaped portion of the spermatheca near the region where it opens into the common oviduct: *ep*, epithelium; *b*, bristle; *p*, primary layer of chitin; *s*, secondary layer of chitin. (x647).

Fig. 3. Longitudinal section of the dorsal part of common oviduct posterior to the entrance of the spermatheca: *ep*, epithelium; *ch*, chitinous intima; *b*, bristles. (x900.)

Fig. 4. Longitudinal section of the chitinous intima of the spermatheca, showing the change in direction of the bristles at *a*, near the constriction *e*, which divides the spermatheca into the heart-shaped dorsal portion and the funnel-shaped ventral part: *v*, bristle near the constriction and pointing ventrally; *d*, bristle below constriction and pointing dorsally; *b*, bristle dorsal to the constriction, these bristles being arranged irregularly upon the unfolded chitin; *p*, primary layer of chitin; *s*, secondary layer of chitin; *c*, pore canal. (x520).

Fig. 5. Cross section of a fold of the oviduct with the peritoneum not shown: *ch*, chitinous intima; *b*, bristles; *ep*, epithelium; *lm*, longitudinal muscles; *cm*, circular muscles. (x647).

Fig. 6. Longitudinal section of the cells of the colleterial sac: *n*, nucleus of epithelial cell; *ch*, chitinous intima. (x867.)

Fig. 7. Epithelium and chitinous intima of the dorsal region of the heart-shaped part of the spermatheca: *p*, primary layer of chitin; *s*, secondary layer of chitin; *c*, pore canal; *ls*, longitudinal striations of cytoplasm. (x647.)

Fig. 1.

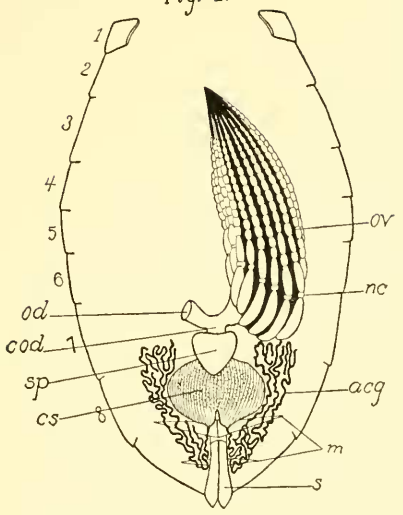


Fig. 2.

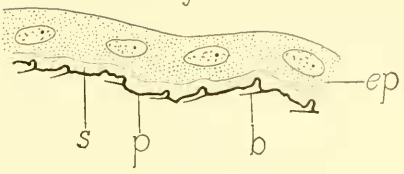


Fig. 3.

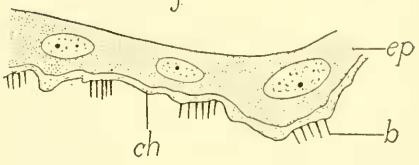


Fig. 5.

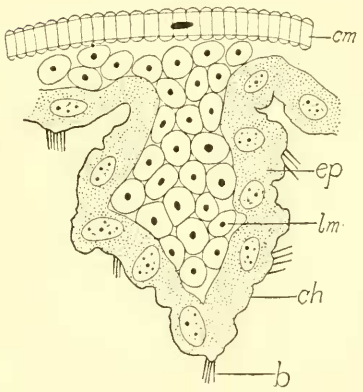


Fig. 4.

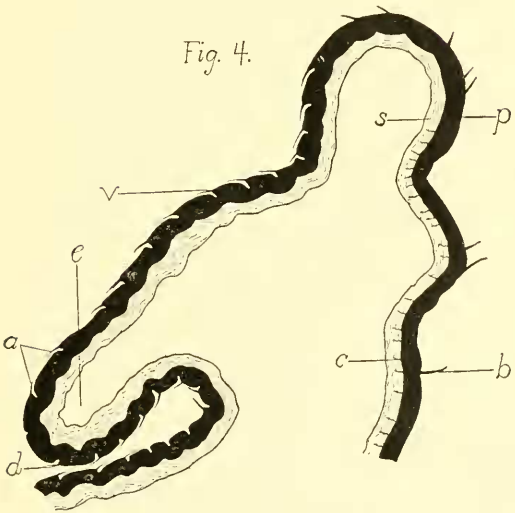
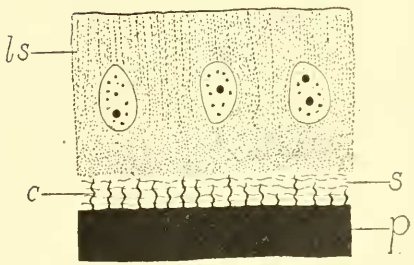


Fig. 7.



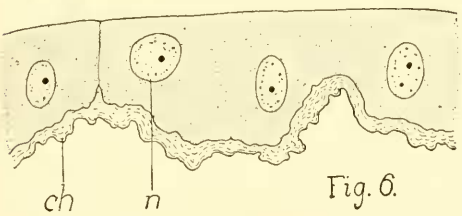


Fig. 6.

Severin.

EXPLANATION OF PLATE IV.

FIG. 8. Longitudinal section through the common colleterial gland duct and colleterial sac, showing the opening of the former into the latter: *o*, opening of the common colleterial gland duct into the colleterial sac; *sp*, spine; *cn*, "endothelial or centro-tubular" nucleus; *n*, epithelial nucleus of the colleterial sac; *c*, canal of "vésicule radiée"; *vr*, "vésicule radiée", "vésicule sécrétante" or "vésicule intracellulaire". (x307.)

FIG. 9. Cross section of cells of the colleterial glands: *ch*, chitinous intima; *cn*, "endothelial or centro-tubular" nuclei; *c*, canal of vesicule radiée; *vr*, "vésicule radiée", "vésicule sécrétante" or "vésicule intracellulaire". (x647.)

FIG. 10. Longitudinal section of cells of the common colleterial gland duct: *ch*, chitinous intima; *c*, canal of "vésicule radiée", *cn*, "endothelial or centro-tubular" nucleus; *vr*, "vésicule radiée", "vésicule sécrétante" or "vésicule intracellulaire"; *ls*, longitudinal striations of cytoplasm; *g*, granular cytoplasm. (x900.)

FIG. 11. Longitudinal section showing the cellular change between the common colleterial gland duct and colleterial sac: *ch*, chitinous intima; *c*, canal of "vésicule radiée"; *cn*, "endothelial or centro-tubular" nucleus; *vr*, "vésicule radiée", "vésicule sécrétante" or "vésicule intracellulaire"; *ep*, nucleus of epithelial cell; *ls*, longitudinal striations of cytoplasm; *g*, granular cytoplasm; *a*, transition of epithelium of duct to that of sac; *s*, spine; *m*, muscles. (x647.)

FIG. 12. Longitudinal section of the colleterial sac duct: *sc*, secretion; *sp*, spine; *ch*, chitinous intima; *m*, muscles of sac that pass into the ventral fold of duct and, spreading out fan-shape, attach to the chitinous intima. (x120)

Fig. 8.

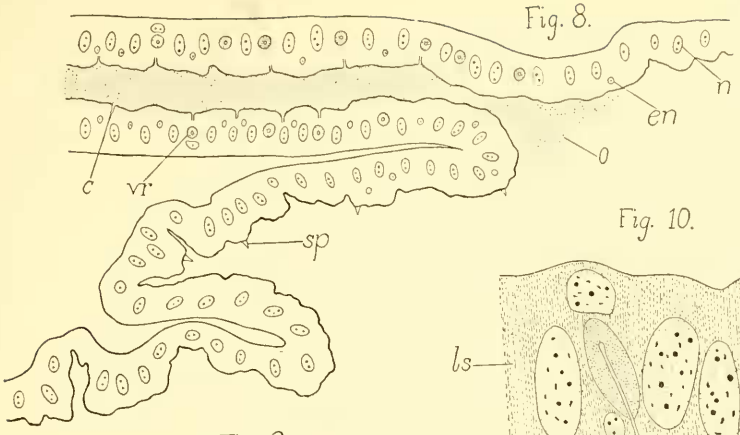


Fig. 10.

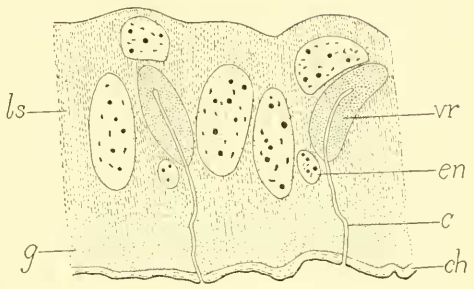


Fig. 9.

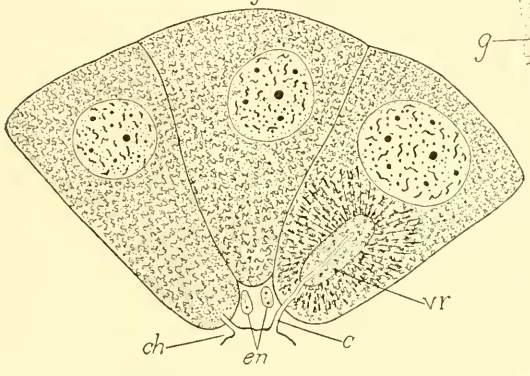
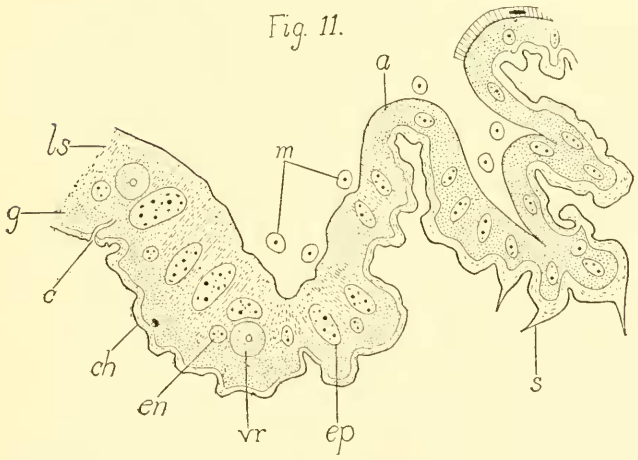


Fig. 12.

Fig. 11.



Severin.

EXPLANATION OF PLATE V.

FIG. 13. Ventral view of saws spread apart, showing the opening of the colleterial sac duct at *d*: *tp*, triangular chitinous plate to which bundles of muscles attach; *vf*, ventral fold; *dl*, lobes that are in continuation with the colleterial sac duct dorsally; *tm*, bundle of transverse muscles which leave the colleterial sac duct dorsally and attach to the basal margin of the sheaths of the saw; *ch*, chitinous intima of colleterial sac duct, to which the transverse muscle fibres attach; *t*, teeth of saw. (x12).

FIG. 14. Cross section of the colleterial sac duct near its opening, showing the attachment of some of the transverse muscles to the dorsal wall of the duct: *tm*, transverse muscle bundles; *n*, nucleus of epithelial cell; *ch*, chitinous intima. (x175.)

FIG. 15. Transverse section of colleterial sac duct nearer to the sac than figure 14, showing the ventral median-groove: *n*, nucleus of epithelial cell; *ch*, chitinous intima. (x175.)

FIG. 16. Last sternite showing the vaginal orifice, *vo*. (x6½.)

FIG. 17. Posterior view of colleterial sac: *cd*, colleterial gland duct; *ccd*, common colleterial gland duct; *o*, opening of common colleterial gland duct into the colleterial sac; *tm*, bundles of transverse muscles which leave the duct and attach to the basal margin of the sheaths of the saws; *l*, lobes that are in continuation with the colleterial sac duct dorsally.

FIG. 18. Diagram showing the common oviduct, spermatheca and colleterial sac with their openings: *cod*, common oviduct; *sp*, heart-shaped part of spermatheca; *f*, funnel-shaped part of spermatheca; *o*, opening of spermatheca into the dorsal wall of the common oviduct; *chp*, triangular chitinous plate; *cs*, colleterial sac; *ccd*, common colleterial gland duct opening into the colleterial sac; *d*, duct of colleterial sac, which opens between the saws; *s*, opening of common oviduct; arrows in the common oviduct indicate the path which the eggs take; the eggs thus pass beneath the opening of the spermatheca at *o*, and, after passing out of the vagina, are received by the saws at *s*. (x20.)

Fig. 13.

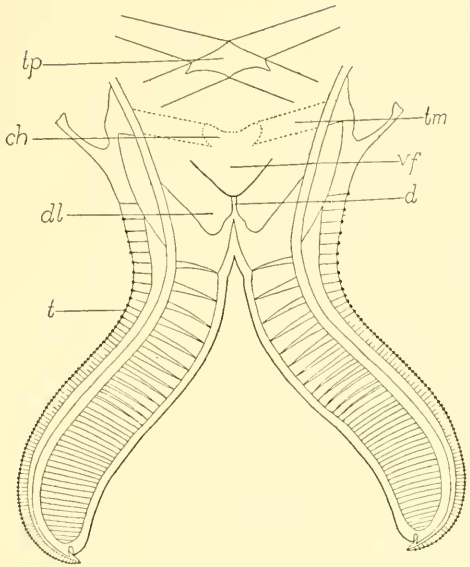


Fig. 14.

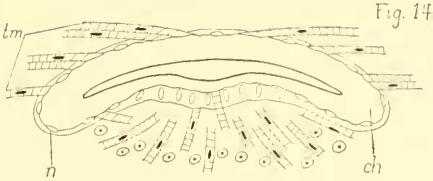


Fig. 15.

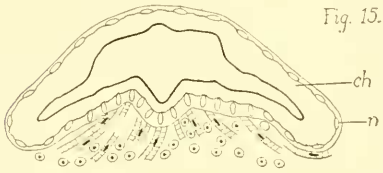


Fig. 16.

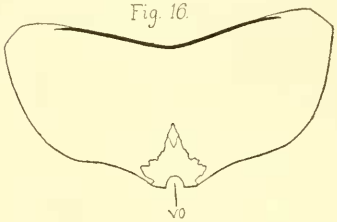


Fig. 17.

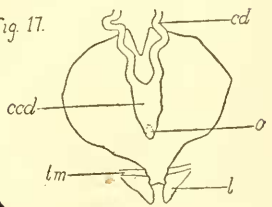
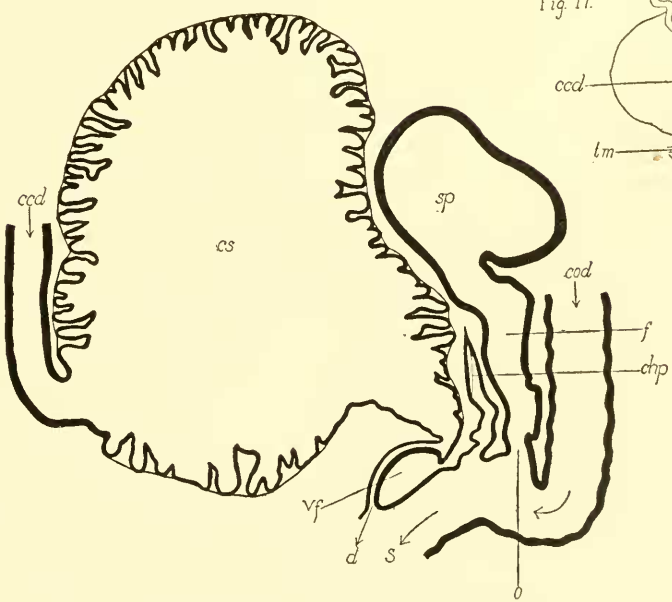


Fig. 18.



Severin.